Capturing Evolution and Ecology in a Global Ocean Model

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Outline

• Challenges
  – Motivating scientific questions

• Approach
  – Existing models and their limitations
  – EVolutionary Ecosystem (EVE) model

• Results
  – Emergent phytoplankton growth strategies
  – Cell size, N:P composition, dynamic storage
How have Earth and life co-evolved in the past?

Shields-Zhou & Och (2011)

Ridgwell & Zeebe (2011)

Mass extinctions
How will the (rest of the) biosphere respond to anthropogenic global change?

How can we use (molecular) biological data to produce better predictive biosphere models?
Overarching challenges

- Life is (very) diverse
- Life adapts
  - Organisms acclimate
  - Populations evolve by natural selection
- Organisms have life histories
- Evolution is contingent
Traditional approaches to modelling the marine ecosystem

Aggregated models - effective locally when tuned to observations in a region of space and time ...but not portable
Limitations of traditional models

• Lack of diversity
• Fixed responses
  – No acclimation or adaptation
• Lack of life histories
  – Important for storage and acclimation strategies in dynamic environments, seasonality, dispersal
• Lack of evolutionary contingency
  – Can access anywhere in trait space

Pygmalion and Galatea by Pecheux (1784)
“A biodiversity-inspired approach to aquatic ecosystem modelling”

“Emergent biogeography of microbial communities in a model ocean”

Total phytoplankton biomass ($\mu$M P, 0 to 50 m average)

Group locally dominating annual mean biomass:
- analogs of *Prochlorococcus*
- other small photo-autotrophs
- Diatoms
- other large phytoplankton

Total biomass of *Prochlorococcus* analogs ($\mu$M P, 0 to 50 m average)
Evolutionary ecology: Traits, trade-offs, emergent strategies

Terrestrial plants

Bloom (1985), Tilman (1990)

Phytoplankton

Shuter (1979), Raven (1984), Vallino et al. (1996)
EVolutionary Ecosystem (EVE) Model Approach

• Individuals:
  – Functional traits
  – Physiologically constrained model organisms
  – Trade-offs and resource allocation

• Community and ecosystem:
  – Selection in model environment
  – Interactions and trophic structure
  – Community assembly (dispersal...)
  – Biogeochemical cycles
Conserved, phylogenetically-related building blocks

Land plants

Chlorophyta

Alveolates

N2 fix

PSII

P uptake

Rubisco

Cell memb

PO4 storage

DNA

S mol biosyn

L mol biosyn

Diatoms

Storage vacuole

Silica armour

30 μM

Physiology, ‘cellular economics’

Monod-type models

Growth
Nutrients
Monod (1942)

EVE model

Inspired by Shuter (1979)

Metabolic networks (systems biology)

Dufresne (2003)

Parameter-sparse representation of diversity and adaptation based on common physiology
Functional traits and trade-offs

Phytoplankton traits

Ecological function

<table>
<thead>
<tr>
<th>Reproduction</th>
<th>Resource acquisition</th>
<th>Predator avoidance</th>
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<tbody>
<tr>
<td>Cell size</td>
<td>Cell shape</td>
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<td>Colonality</td>
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Trait space

Trade-offs emerge from physiological constraints and cost-benefit

Environmental selection

Organisms: Agents in trait space

Environment: MIT gcm

Dispersal
Drift
Mutation

Biotic interactions

Environmental filter

Response traits

Effect traits

Ecosystem structure and function

- Size
- Composition

PGS

POP
DOP
DIP
Applications

• Emergent phytoplankton growth strategies and biogeography

1. Cell (minimum) size
2. Composition and N:P stoichiometry
3. Dynamic strategies
1. Patterns in phytoplankton size

Biogeography (Alvain 2008)

- **Oligotrophs / gleaners**
  - ‘K strategists’
  - Nutrient limited
  - < 1μm prokaryotes
  - 95% efficient microbial loop
  - \( R^* \), small size

- **Copiotrophs / opportunists**
  - ‘r strategists’
  - Light-limited
  - >10 μm eukaryotes

**Growth rate**
**Storage strategies**

- **Pico** < 2 μm
- **Nano** 2 - 20 μm
- **Micro** 20 – 200 μm
Model and minimum size constraint

2D Trait space $S(r) + E + L = 1$

Photosynthesis max rate $f_P = \kappa_P \frac{I L_{res}}{m}$

Biosynthesis max rate $f_S = \kappa_S E_{res} Q_{10}^{(T-T_0)/10}$

Nutrient uptake max rate $f_N = \kappa_N \frac{c_\infty}{r^2}$

Growth rate $\mu = \min(f_P, f_S, f_N)$ - maintenance

Cell size and adaptation to low light (BATS)

Shift to larger cell sizes (~0.7 μm) in *Prochlorococcus* during the spring bloom.

Larger cell sizes generally observed at depth, around the deep chlorophyll maximum.

- High light adapted species dominate in well mixed surface waters.
- In stratified conditions, shift to low light adapted species at depth.

**DuRand (2001)**

**Malmstrom (2010)**

Abundance

High light adapted species dominate in well mixed surface waters.

In stratified conditions, shift to low light adapted species at depth.
Phytoplankton population dynamics at BATS

Shift to larger cell size

Higher investment in photosynthesis

2. Patterns in phytoplankton N:P stoichiometry

Phytoplankton stoichiometry in laboratory culture

N:P from diatom (Si export) weighting (Weber & Deutsch 2012)

N:P from chl and size-class weighting (Daines et al. 2013)

‘Greens’
Ostreococcus
Prokaryotes:
Prochl.
Synecococcus

‘Reds’
Diatoms
Cocolithophores

N:P from diatom (Si export) weighting (Weber & Deutsch 2012)
The growth rate hypothesis, rRNA and N:P

• Maintaining high growth rates requires high concentrations of P-rich ribosomes (rRNA)
• Predict that faster growth rate produces lower N:P organisms
• Crucial to determining how low N:P can go is the rRNA ‘rate constant’ for protein synthesis (aa rib$^{-1}$ s$^{-1}$)

rRNA required for protein synthesis

- Existing models span a range 2.7–5.7 aa rib⁻¹ s⁻¹
- High value is from yeast (heterotrophic fungus!)
- New compilation of data for photoautotrophs
Predictions from the growth rate hypothesis

- Explains overall patterns in N:P
- But not lowest observed N:P
- Additional contribution from P storage?

Daines, Clark, Lenton (2013) *Ecol. Lett.* in review

Data Weber & Deutsch (2012)
Physiological effect of warming

- Rate of protein synthesis increases strongly with temperature
- Less P-rich ribosomes required to produce required N-rich protein at higher T
- Therefore physiological effect of warming is to increase organism N:P
- But must also consider effects of increased stratification reducing nutrient supply...
3. Strategies for dynamic environments

- Autotroph storage pools even out stochastic supply of light, N, P
- But how to model this?...

e.g. Fluctuating light environment in mixed layer (Ross et al. 2008)

Storage and acclimation as optimal control

• Fitness benefit of dynamic allocation (acclimation, storage)

$$J^*_k(x_k, e_k) = \max_{u_k} E \left\{ g_k(x_k, e_k, u_k(x_k, e_k), w_k) + J^*_{k+1}(F_k(x_k, e_k, u_k, w_k)) \right\}$$

Fitness (eg biomass)  
Instantaneous benefit  
Future benefit
One optimal strategy in constant environment – no C storage
Emergent strategies in fluctuating environments

Slow variability – C storage over diel cycle, acclimation

cf Ross & Geider (2009)

Fast variability – fitness maximisation
⇒ increased allocation to Rubisco, C storage buffering of short light pulses

Daines (2013) *Am. Nat.* in revision
Summary

• Approach of physiology + resource allocation + optimality gives a parameter-sparse representation of diversity:
  – Environmental selection on traits (population adaptation)
  – Dynamic environments: fitness maximising behaviour as optimal control (acclimation, storage strategies)

• Environmental selection for phytoplankton growth strategies
  – Size: Nutrients ⇒ (minimum) size
  – Composition: overall patterns in N:P
  – ... but growth rate requirements for rRNA can only explain part of N:P
  – Dynamic strategies as fitness maximisation

• Functional trait and physiological approach is unreasonably effective ...as an approach to evolutionary ecology
Implications for the carbon cycle

• C:N is relatively conserved therefore predicted increase in N:P under warming implies increased C:P and potentially greater export
  – But need to consider changes in multiple environmental controls
• Increase in phytoplankton N:P will tend to produce more N limitation, but may also select more strongly for diazotrophs
• Need dynamic strategies to capture storage of C, P and N in phytoplankton properly
Integrative Terrestrial-Marine Lessons

• Traits and physiologically-grounded trade-offs is the way forward for process-based prediction (cf Tilman 1990, JeDi terrestrial model)

• Marine: Primary production by microbes in fluid
  – Relatively direct link from cellular economics and ecophysiology to biogeochemical cycles (but recycling still ‘complicated’ and higher organisms and trophic structure important for biological pump)
  – High diversity and rapid adaptation of microbial ecosystem
  – Fluid physical environment ‘easy’ to model

• Terrestrial: Primary production by higher plants in soil
  – Multi-cellular complexity and soil formation means indirect link from ecophysiology and cellular economics to biogeochemical cycles
  – Long lifetimes, slow dispersal, slower adaptation timescales
  – Solid phase of physical environment ‘hard’ to model